

A REVISION OF THE *CHAMAESYCE DELTOIDEA*  
(EUPHORBIACEAE) COMPLEX OF  
SOUTHERN FLORIDA

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ABSTRACT

Morphological investigation of the *Chamaesyce deltoidea* complex demonstrates a lack of sharp boundaries between the taxa. In combination with distributional data, the observed patterns of morphological variation suggest that the complex is best treated as a single polymorphic species. New combinations are proposed for *Chamaesyce pinetorum* and *C. adhaerens* to provide a consistent treatment for the morphological groups within the complex. The current conservation status of each morphological group is reviewed.

Key Words: *Chamaesyce deltoidea*, subspecies complex, endangered species, geographical distinction, south Florida

*Chamaesyce deltoidea* (Engelmann) Small represents a complex of four closely related taxa found in the rocky pinelands south of Miami and similar pinelands on the lower Florida Keys (Figure 1). Three of the taxa are currently listed as endangered (Bentzien, 1985; listed under the name *Euphorbia deltoidea*), and a clear understanding of taxonomic limits within the complex is required for proper application of provisions of the Endangered Species Act. However, current treatment of the group (Burch, 1965, 1966) does not satisfactorily account for patterns of variation found within the complex.

*Euphorbia deltoidea* Engelmann ex Chapman was the first member of the complex to be described. It was included in the appendix (p. 647) of Chapman (1883). This species was transferred to the genus *Chamaesyce* by Small (1903, p. 710, 1033). During the following three decades, Small proposed three new species closely related to *C. deltoidea*: *C. pinetorum* (Small, 1905), *S. serpyllum* (Small, 1913, p. 81, 155), and *C. adhaerens* (Small, 1927). Members of the complex are characterized by wiry stems radiating from a woody taproot, thick leaves with shallowly cordate bases, cyathia on short peduncles solitary in leaf axils, and minute or absent gland appendages. These four taxa are endemic to southern Florida. Several West Indian species, particularly *C.*

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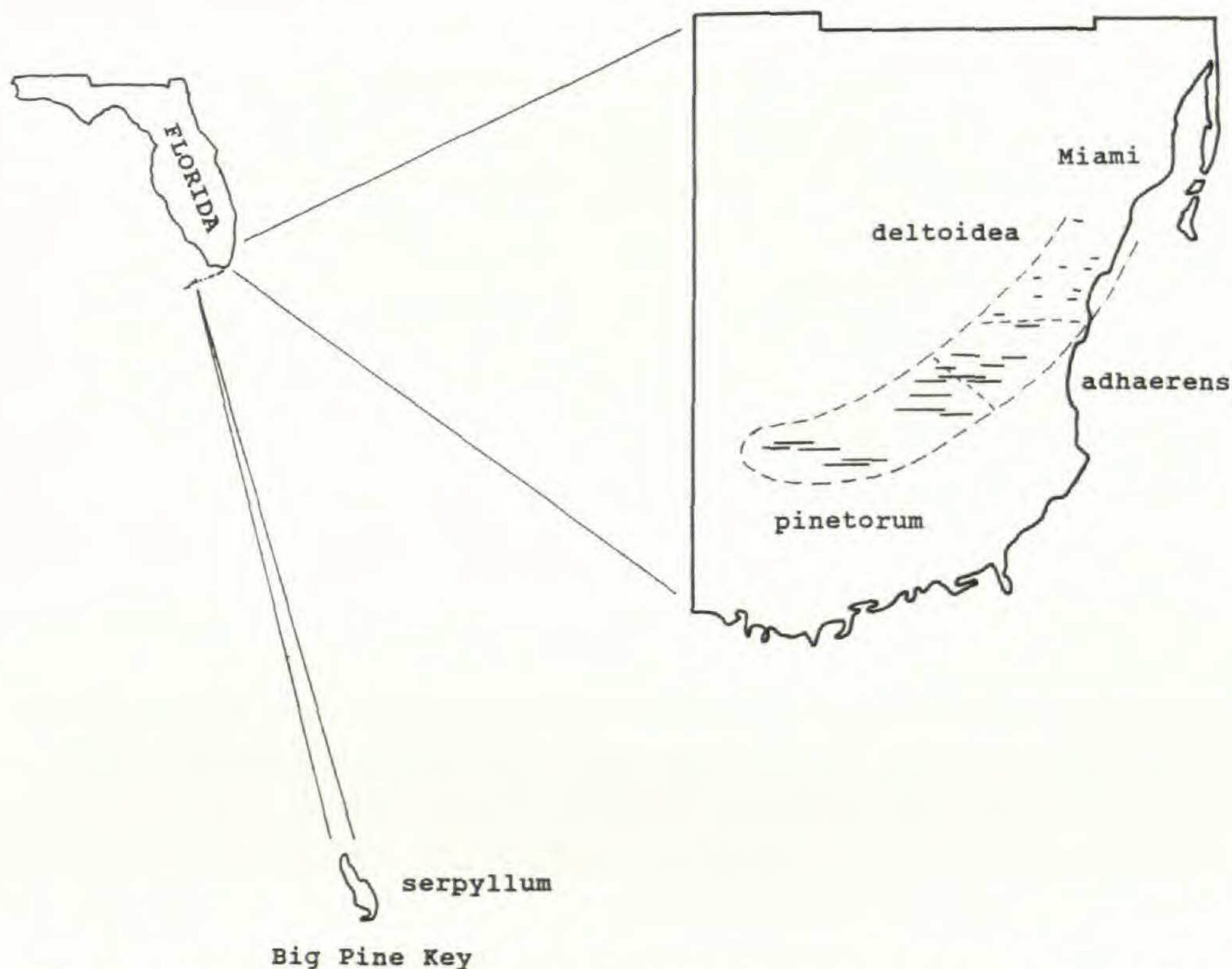


Figure 1. Map of southern Florida showing geographical distribution of the four subspecies in the *Chamaesyce deltoidea* complex, and distribution in trichome lengths for the three mainland subspecies. Each bar represents a separate population; length of bar is proportional to length of stem and leaf trichomes in the population. Only populations with accurately known locations are mapped.

*turpinii* (Boissier) Millspaugh [including *C. puertoricensis* (Urban) Millspaugh] and *C. centunculoides* (H.B.K.) Millspaugh are closely related to the *C. deltoidea* complex, but are easily distinguished by possession of gland appendages equalling or exceeding the gland in width.

In Small's final treatment of the complex (Small, 1933), each member was considered to represent a distinct species. Major characters used to define the species were habit and pubescence. Minor distinctions were also noted in seed and cyathium characters (Table 1). More recently, Burch (1966) grouped the four members of the complex into two species distinguished from each other by habit. *Chamaesyce deltoidea* included all populations having prostrate stems (Small's *C. adhaerens*, *C. deltoidea* and *C. serpyllum*) while *C. pinetorum* included all plants with erect or ascending stems. This treatment was adopted by Long and Lakela (1971). The most recent study of this complex was that of Remus (1979), and it purported to support Burch's treatment.

Table 1. Characters used by Small (1933) in distinguishing among the taxa of the *Chamaesyce deltoidea* complex.

Character	<i>C. adhaerens</i>	<i>C. deltoidea</i>	<i>C. pinetorum</i>	<i>C. serpyllum</i>
Habit	prostrate	prostrate	ascending	prostrate
Pubescence	villous-hirsutulose	glabrous	villous-hirsute	puberulent-canescent
Leaf shape	as long as wide	as long as wide	———*	longer than wide
Cyathium length	about 1 mm	less than 1 mm	1 mm	less than 1 mm
Seed length	about 1 mm	less than 1 mm	1 mm	less than 1 mm

\* This character not reported by Small.

However, Remus used the name *Chamaesyce adhaerens* for different plants than Small, and his conclusions actually imply a closer relationship between Small's *C. adhaerens* and *C. pinetorum* than between *C. adhaerens* and *C. deltoidea*.

In this study, a modified key for identification of the taxa is presented and relationships between taxa are discussed. The four taxa of Small are all treated as subspecies of *Chamaesyce deltoidea*. Only the subspecies designations are referred to in the text below.

#### MATERIALS AND METHODS

A survey of all extant potential habitat was carried out during the years 1980–81. Materials from throughout the current range of the taxa were collected for analysis during this study. Additional herbarium specimens were borrowed to supplement these collections. A total of 277 specimens was examined.

Several characters were measured on dried specimens. Leaf length was measured along the midvein and leaf width was measured perpendicular to the midvein at the widest point of the leaf on up to five fully-exposed, flat leaves per sheet. Cyathium length and width (measured across the glands) were measured for up to seven cyathia per sheet. When available, cyathia with staminate or pistillate flowers at anthesis were measured, otherwise cyathia with young or mature fruit were measured. Seed length was measured along the long axis of the seed using an optical comparator. Trichome length was measured or, when the trichomes were curved or bent, estimated on stem, leaves and cyathia using an optical

comparator. Trichome density on stems and leaves was scored following the method of Isley (1953) where samples were assigned to density classes on the basis of the ratio between average trichome length and the average distance between trichomes. The youngest fully expanded leaves and the stem sections immediately below them were used for trichome density estimates. Trichome length was most conveniently measured near the tip of a stem.

Specimens preserved in Formalin–Acetic Acid–Alcohol or 95% Ethyl Alcohol were available for several populations covering the entire current range of the complex. Cyathium length and width measurements were taken from these specimens to verify and supplement results obtained from dried specimens.

#### RESULTS

Bar graphs of seed length (Figure 2) show a large degree of overlap among all four taxa. Seed length in *ssp. serpyllum* averages lower than in the other three subspecies, but the significance of this difference is obscured by the large degree of overlap with other subspecies. In the other characters used by Small, a similar picture is presented. In the few cases where average differences are found between subspecies, such as leaf shape, where *ssp. serpyllum* has narrower leaves in general than other taxa, overlap between taxa is extensive.

Cyathium width proved to be an unsatisfactory character to measure from dried specimens due to variations in the amount of pressure on different cyathia during drying. Measurements taken from liquid-preserved material (Figure 3) showed that variation within populations was always high and often a large fraction of the total variation found within the complex. No consistent differences in cyathium size or shape were found to separate the taxa.

Populations of *ssp. deltoidea*, *ssp. pinetorum* and *ssp. serpyllum* are easily identifiable, each having a distinct set of morphological characteristics. Subspecies *deltoidea* is characterized by prostrate stems, a predominantly short-shoot growth form with internodes shorter than leaf width, stems and leaves glabrous or very sparingly pubescent, and appressed uncinata trichomes. Subspecies *pinetorum* has erect or ascending stems, a predominantly long-shoot growth form with internodes usually 1.5 to 2 × leaf width, and a dense covering of long, straight, spreading hairs. Subspecies

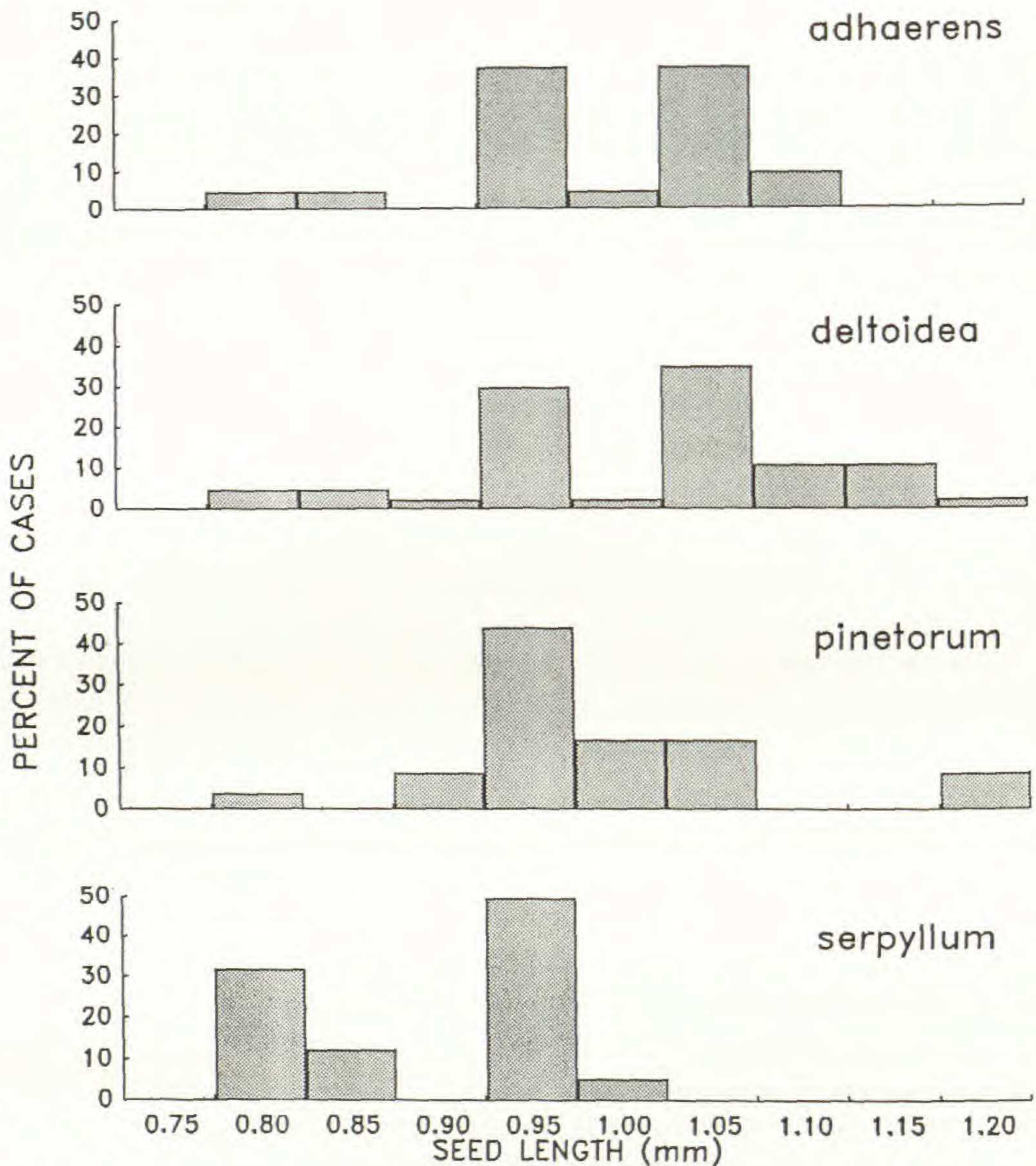


Figure 2. Bar graphs showing distribution of seed lengths in the four subspecies of the *Chamaesyce deltoidea* complex (based on measurements of 25 seeds for each subspecies). Degree of overlap demonstrates that this character cannot be used to distinguish among the taxa.

*serpyllum* is characterized by prostrate stems, a predominantly long-shoot growth form, and a very dense pubescence (which gives the plant a silvery appearance) of appressed, irregularly twisted trichomes.

Subspecies *adhaerens* is here defined in terms of pubescence characters alone. It has appressed uncinuate trichomes on leaf surfaces and twisted, ascending to spreading, trichomes on stem surfaces. Trichome length, trichome density and plant habit vary in a clinal fashion across the range of ssp. *adhaerens*. At the

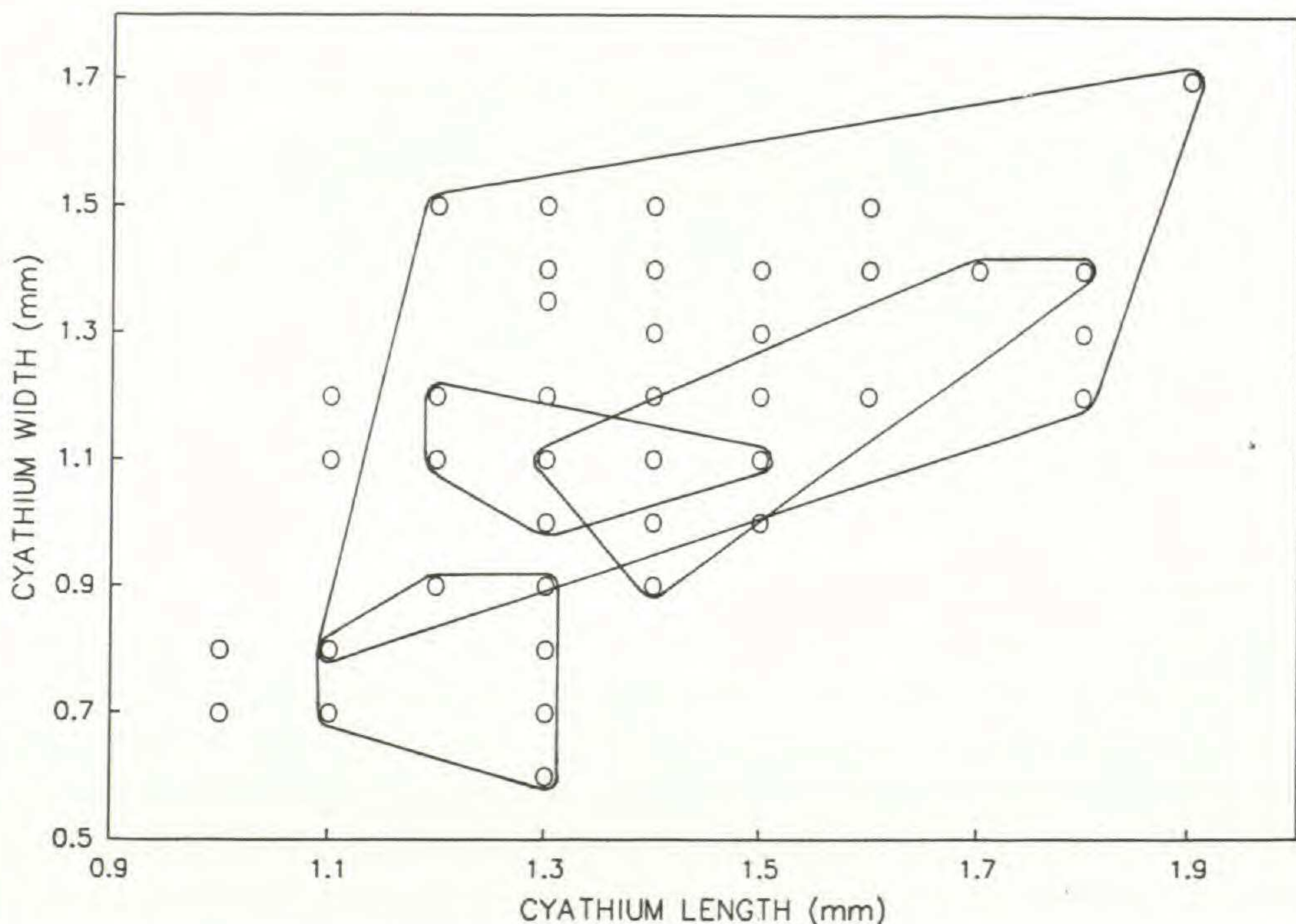


Figure 3. Scatter diagram of length and width measurements taken from liquid-preserved cyathia. Curves enclose measurements from four populations. Variability within single populations is often a large fraction of the total variability observed in the complex.

northern end of its range it approaches *ssp. deltoidea* in appearance, and at the southern end, it grades into *ssp. pinetorum*.

#### DISCUSSION

Subspecies *pinetorum* is not isolated from other members of the complex as the current classification (Burch, 1966) implies; it forms an evolutionary unit equivalent to *ssp. deltoidea* or *ssp. serpyllum*. The taxonomic rank of the three groups of populations is hard to define. They are more strongly differentiated than most subspecific taxa, and, if *ssp. adhaerens* were not present, could easily be considered weakly separated species. But, for the reasons given below, I treat them here as members of a single polymorphic species.

The differences between all four members of the complex are vegetative and no differences have been found in their life histories or modes of reproduction. The vegetative characters used to define the differences are found to vary in a clinal fashion in the mainland populations, and these populations seem to inter-

grade along broad zones of contact. Differences between the populations of *ssp. serpyllum* on the Florida Keys and the mainland subspecies are no different in kind than the differences between the extreme forms of the mainland subspecies. Finally, there is no geographical overlap of different morphological types to suggest barriers to interbreeding. One specimen of *ssp. adhaerens* preserved at NY (*Small & Carter 860*) indicates a collection locality (by an arrow drawn on a map of Dade Co.) within the range I have defined for *ssp. pinetorum*. Another specimen of *ssp. deltoidea* at NY (*Small & Wilson 1979*) similarly indicates a collection locality outside of the range shown for *ssp. deltoidea* in Figure 1. No detailed information on the locality of either collection has been located nor has any reference by Small to finding any subspecies growing together. Burch (1965) stated that *ssp. pinetorum* is broadly sympatric with *ssp. adhaerens* and *ssp. deltoidea*, but this assertion is not supported by any specimens I have seen. Since neither the precisely located collections of Burch nor my own field survey produced any examples of two members of the complex growing together, I do not consider these suggestions of range overlap credible.

In addition to the arguments presented above, it is relevant that qualitative differences in pubescence can be found within other species of *Chamaesyce*. In particular, *C. turpinii*, as presently understood, has essentially the same range of pubescence types as do pubescent forms of *C. deltoidea*. In a different group, the current conception of *C. polycarpa* (Bentham) Millspaugh encompasses both glabrous and pubescent plants.

Populations of *ssp. adhaerens* bridge the morphological gaps between the other three taxa. Stem habit within this taxon ranges from appressed to ascending and a mixture of long-shoots and short-shoots is often found on a single plant. The only characteristic that consistently separates *ssp. adhaerens* from *ssp. deltoidea* on one hand and *ssp. pinetorum* on the other is the occurrence of irregularly twisted hairs in stem pubescence. It differs from *ssp. serpyllum* in having less dense pubescence with only uncinuate trichomes on the leaf surfaces. Geographically, *ssp. adhaerens* occupies the area between *ssp. deltoidea* and *ssp. pinetorum* (Figure 1). When trichome length, plant habit, or pubescence density are considered separately, the values found in populations of *ssp. adhaerens* smoothly bridge the gap between *ssp. deltoidea* and *ssp. pinetorum*. Close inspection of Figure 1

suggests that there is an abrupt change in trichome length at the boundary between ssp. *deltoidea* and ssp. *adhaerens*, but specimens with intermediate trichome length exist (*Lakela & Almeda 30450* and *Lakela & Pardue 31583*) that are not mapped because their locations are not accurately known.

The phylogenetic relationships of ssp. *adhaerens* within the complex are not fully clear. Currently, ssp. *adhaerens* is represented by a small series of populations intermediate in morphological features between ssp. *deltoidea* and ssp. *pinetorum*. Also, ssp. *adhaerens* is much more uniform morphologically within populations and has larger differences between populations than the other three taxa of the complex. This pattern of variation suggests that relatively recent hybridization between ssp. *deltoidea* and ssp. *pinetorum* might have given rise to ssp. *adhaerens*. Such a scenario is also supported by the apparent intergradation of ssp. *adhaerens* with those two along its borders. However, hybridization would only be possible if the putative parents were growing in much closer proximity than they are currently. Alternatively, it is possible that the pattern of variation reflects local adaptation to varying environmental factors, such as differences in soil type or water availability. Changes in substrate conditions are at least loosely correlated with the changes in morphological pattern. The range of ssp. *deltoidea* corresponds to that area of the Miami Rock Ridge overlain with a thin layer of white sand (Snyder et al., 1990). The ssp. *adhaerens* occurs in the area with a reddish sandy loam while ssp. *pinetorum* is largely found in the lower, wetter pinelands at the southwestern end of the Miami Rock Ridge. Unfortunately, the pinelands habitat of the complex has been so fragmented and reduced over the past decades that it is no longer possible to make detailed studies to compare these two hypotheses. In particular, the zones where the taxa would have met historically have been obliterated, so the abruptness of the transitions cannot be assessed. It is also possible that the patterns of variation seen in present populations of ssp. *adhaerens* may reflect accidents of preservation more than historical patterns. Despite the uncertainty, I consider the hypothesis of local differentiation more probable on the basis of current evidence.

As noted above, ssp. *adhaerens* does not have the morphological distinctiveness of the other members of the complex. Still, the populations are in most cases easily distinguished from the other taxa and occupy a significant portion of the range of the



complex (Figure 1). The combination proposed by Burch in 1966 (*Chamaesyce deltoidea* ssp. *deltoidea* var. *adhaerens*) does not adequately describe the position of ssp. *adhaerens* within the complex. In particular, there is no reason to believe that ssp. *adhaerens* is more closely related to ssp. *deltoidea* than it is to ssp. *pinetorum*. For these reasons, and in accordance with the hypothesis that the various morphological types all arose independently through adaptation to local conditions, I use the rank of subspecies for all taxa in the complex.

#### TAXONOMIC TREATMENT

### *Chamaesyce deltoidea* (Engelmann ex Chapman) Small

Plants herbaceous, stems 10–15 cm long, wiry, radiating from a woody taproot, appressed to the ground surface or ascending to erect. Leaves reniform to ovate; thick, obscuring secondary venation; bases strongly inequilateral, commonly shallowly cordate; margins entire, thickened, usually inrolled. Stipules membranaceous; usually joined to base and deltoid in outline, often lacerate or lobed, sometimes split fully to the base; white to reddish; inconspicuous. Inflorescences solitary in leaf axils. Peduncle shorter than to slightly exceeding the leaf. Cyathia glabrous to densely pubescent, involucre campanulate, .9 to 1.9 mm long, .5 to 1.7 mm wide, lobes triangular, equalling to slightly exceeding the glands. Glands elliptic, .4 mm long, .3 mm wide. Gland appendages minute or lacking. Capsule glabrous to densely pubescent, about 1.3 mm long. Seeds about 1 mm long, quadrate, brown, the flat surfaces usually having 3–4 shallow (sometimes inconspicuous) ridges.

#### KEY TO SUBSPECIFIC TAXA OF *CHAMAESYCE DELTOIDEA*

1. Stems erect or ascending
  2. Pubescence of leaves spreading, .6–.7 mm long, straight; pubescence of stems same . . . . . 3. ssp. *pinetorum*
  2. Pubescence of leaves appressed, .1–.25 mm long; pubescence of stem spreading or ascending, .1–.25 mm long, irregularly twisted . . . . . 2. ssp. *adhaerens*
1. Stems prostrate or appressed to ground surface
  3. Pubescence of leaves sparse, appressed; stems glabrous or thinly pubescent; hairs on leaves uncinata; hairs on stems uncinata . . . . . 1. ssp. *deltoidea*

3. Pubescence of leaves dense, appressed to spreading; pubescence of stems dense; hairs on leaves uncinata or irregularly twisted; hairs on stems irregularly twisted
4. Pubescence of leaves composed of irregularly twisted hairs; plants appearing silver or gray ..... 4. ssp. *serpyllum*
4. Pubescence of leaves uncinata; plants bright green ... 2. ssp. *adhaerens*

1. ***Chamaesyce deltoidea*** (Engelmann ex Chapman) Small ssp. ***deltoidea***, Fl. Southeastern U.S., p. 710, 1903.

*Euphorbia deltoidea* Engelmann ex Chapman, Flora of the Southern U.S., ed. 2, p. 647, 1883. TYPE: United States. Florida [Dade Co.], rocky pine woods, Bay Biscayne, June, *Curtiss 2474\** (LECTOTYPE: MO (1792963)! (herein designated); ISOTYPES: CU!, GH!, MIN!, NCBS!, NY [3 sheets]!, PH [2 sheets]!, US [2 sheets]!)

Plants forming small mats with stems and leaves appressed to ground surface, bright green. Margins of adjacent leaves on most stems typically overlapping. Stems glabrous or very sparsely pubescent with appressed, uncinata trichomes .10–.25 mm in length. Leaves usually glabrous above, often sparsely pubescent beneath with appressed, uncinata trichomes .10–.25 mm in length. Cyathia and capsules glabrous to sparsely pubescent.

Although Chapman credited Engelmann with this species, comparison of the published description (Chapman, 1883) with the specimen in the Engelmann herbarium (MO 1792963) and with a manuscript description by Engelmann (MO archives, Engelmann collection), shows that Chapman's description was derived independently. The Engelmann name was known to Chapman from one or more specimens in the exsiccata series North American Plants distributed by A. H. Curtiss (*Curtiss 2474\**). All replicates of *Curtiss 2474\** that could be located in this country were examined, but none was found that could be identified with the specimen Chapman used in drawing up his description. Burch annotated the specimen in the Engelmann herbarium as lectotype for the species, and I accept this choice. The remaining replicates of *Curtiss 2474\** have traditionally been treated as isotypes. Exsiccata numbers in this series are not equivalent to collection numbers, but \* and \*\* are appended to exsiccata numbers elsewhere in the series to denote different collections of the same species.

Also, specimens of *Curtiss 2474\** I have seen are consistent with replicates from a single gathering, so I accept them as isotypes. The year of collection of *Curtiss 2474\** remains uncertain, but annotations on sheets received by Engelmann and the U.S. Department of Agriculture suggest that the specimens were collected in 1880.

This is the most northerly taxon in the complex. Its historical range was in the dry Miami Rock Ridge Pinelands from about the center of Miami to some 13 miles south. All but a few remnants of this pineland area have been converted to commercial or residential use. In those remnants, the *Chamaesyce* grows in a thin layer of white sand over limestone bedrock. It is most abundant in areas free of shrubby undergrowth. Most of the remaining populations are found on lands owned by the federal, state or local governments, and, given protection from development as well as periodic burns to keep the pinelands open, should persist indefinitely. Management regimes imposed in these pineland remnants, however, could affect survival of the populations in unforeseeable ways. Continued population monitoring will be necessary to provide sufficient warning of potential adverse effects.

REPRESENTATIVE SPECIMENS: UNITED STATES. **Florida:** Dade Co., pinelands north of Goulds, 10 Aug 1963, *Burch 144a* (FLAS, MO, NY); rocky pine woods near Miami, 11 July 1895, *Curtiss 5468* (F, FLAS, GH, MIN, NY, US); Miami, July 1877, *Garber sn* (F, FLAS [2 sheets], GH, NY, US [2 sheets]); in dry sandy pineland, Buena Vista, 26 Dec 1929, *Moldenke 291* (MO, NY, PH, US); Miami, 13 May 1904, *Tracy 9114* (CU, F, GH, MIN, MO, NY, PH, US).

2. ***Chamaesyce deltoidea* ssp. *adhaerens*** (Small) Herndon, *comb. et stat. nov.*

*Chamaesyce adhaerens* Small, *Torreyia* 27: 104. 1927. TYPE: United States. Florida, Dade Co., pinelands between Peters Prairie and Homestead, 10 Nov 1906, *Small & Carter 2531* (HOLOTYPE: NY!).

Stems and leaves appressed to ground surface and plants forming small mats or stems ascending and plants forming small tufts. Margins of adjacent leaves on most stems overlapping. Stems pubescent with ascending to spreading, irregularly bent trichomes .25–.55 mm in length. Leaf trichomes nearly the same length but appressed, uncinata.

As discussed in the text, this taxon occupies the gap between

ssp. *deltoidea* and ssp. *pinetorum* both geographically and morphologically. It is found in the Redlands area of Dade Co. where it grows on a fine, reddish sandy loam over limestone bedrock in remnants of the Miami Rock Ridge Pinelands. It is the rarest taxon in the complex, and the one most likely to be lost because no known populations are found on protected lands.

REPRESENTATIVE SPECIMENS: UNITED STATES. **Florida:** Dade Co., badly burned pinelands on south side of Bauer Dr., east of Krome Ave., 3 May 1978, *Avery 1884* (Everglades National Park, FLAS, USF); open pineland near Homestead, 16 Apr 1964, *Burch & Ward 271* (F, GH, MO); open pine-palmetto forest, Homestead, 9 Aug 1980, *Herndon 402* (FLAS, FTG; also distributed to JBSD, NCU, TEX, US); Pinelands, near Murden Hammock, 22 June 1915, *Small, Mosier & Small 6451* (FLAS, GH, NY).

3. ***Chamaesyce deltoidea* ssp. *pinetorum*** (Small) Herndon, *comb. et stat. nov.*

*Chamaesyce pinetorum* Small, Bull. N.Y. Bot. Gard. 3: 4. 1905. TYPE: United States. Florida, Dade Co., Pinelands near the homestead road, between Cutler and Longview Camp, 9–12 Nov 1903, *Small & Carter 836* (HOLOTYPE: NY!; ISOTYPE: PH!). *Euphorbia smallii* Oudejans, Phytologia 67: 236, 1989.

Plants forming small tufts. Stems ascending to erect, usually red. Margins of adjacent leaves on most stems not overlapping. Stems, leaves, and capsules villous, with straight, spreading trichomes .6–.7 mm in length.

In addition to the easily identified holotype and isotype, there are a few more potential isotypes which should be noted. These specimens have the same label data as *Small & Carter 836*, but do not have a collection number. One such sheet at US was annotated as an isotype by Burch.

Strongly upright, often red stems give this plant a highly distinctive appearance. It grows in rarely flooded pinelands, although it seems to grow in slightly wetter areas than the other three taxa. This subspecies is currently the most abundant of the complex, primarily because almost a quarter of its original range falls within the boundaries of Everglades National Park. It is protected from direct habitat destruction, but its survival may be dependent upon the specific fire regime imposed.

REPRESENTATIVE SPECIMENS: UNITED STATES. **Florida:** Dade Co., pinelands near Long Prairie, 24 Mar 1904, *Britton 193* (F, NY); open pine wood, Princeton, 30 Nov 1963, *Burch 232* (FLAS, NY, US); open rocky pinelands, Homestead, 13

Apr 1980, *Herndon 348* (FTG; also distributed to JBSD, NCU, RSA, TEX); open rocky pinelands, Long Pine Key, Everglades National Park, 5 Jun 1981, *Herndon 514* (FLAS, FTG; also distributed to JBSD, NCU, RSA, TEX); Pinelands about Sykes Hammock, 2 Jul 1915, *Small, Mosier & Small 6761* (FLAS, GH, NY).

4. ***Chamaesyce deltoidea* ssp. *serpyllum*** (Small) Burch, *Ann. Missouri Bot. Gard.* 53: 90–99, 1966.

*Chamaesyce serpyllum* Small, *Flora Florida Keys* 81. 1913. TYPE: United States. Florida, Monroe Co., Big Pine Key, 17 Nov 1912, *Small 3811* (HOLOTYPE: NY!). *Euphorbia deltoidea* Engelmann ex Chapman var. *serpyllum* (Small) Oudejans, *Phytologia* 67: 45, 1989.

Stems and leaves appressed to ground surface, forming small silver-green to white mats. Margins of adjacent leaves on most stems not overlapping. Stems, leaves and capsules densely pubescent with appressed to ascending, irregularly bent trichomes .1–.25 mm in length.

The dense, silvery pubescence of this plant blends in amazingly well with the surface of the coral rock it grows on and probably also provides considerable protection against desiccation in the hot, dry pinelands of the lower Florida Keys.

Much of the original range of this subspecies lies within the boundaries of the National Key Deer Refuge and is protected from direct habitat destruction. Continued commercial and residential development in the Florida Keys, however, could adversely affect the subspecies through changes in availability of fresh water or changes in fire regime. Currently, the subspecies is widespread in the pineland areas of Big Pine Key, but the populations are scattered, and the total number of plants does not appear to be large.

REPRESENTATIVE SPECIMENS: UNITED STATES. **Florida:** Monroe Co., occasional in pine woods, Big Pine Key, 10 Aug 1963, *Burch 139* (FLAS, GH [2 sheets], MO, NY); Big Pine Key, 8 Feb 1977, *Correll & Popenoe 48057* (FTG, NY); pine woods, Big Pine Key, 1–17 Feb 1937, *Killip 32062* (GH, MO, US); Pinelands, Big Pine Key, 12 Nov 1912, *Small 3768* (F, NY [2 sheets]); Pinelands, Big Pine Key, 17 Dec 1913, *Small & Small 5027* (F, NY).

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